FINAL REPORT

Title: **What prescribed fire conditions best replicate active fire regimes effects on understory diversity?**

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List of Abbreviations/Acronyms

Abco: *Abies concolor* (white fir)
Abma: *Abies magnifica* (red fir)
BC: Burn/Caspo treatment (all trees >10" and <30" removed followed by a Rx burn)
BN: Burn/No thin treatment (Rx burn, no thinning applied)
BS: Burn/Shelterwood (all trees >10" removed except for 8 trees/ac left evenly spaced, followed by a Rx burn)
Cade: Calocedrus decurrens (incense cedar)
UC: Unburned/Caspo treatment (all trees >10" and <30" removed)
UN: Unburned/No thin treatment (Control)
US: Unburned/Shelterwood (all trees >10" removed except for 8 trees/ac left evenly spaced)
Pije: *Pinus jeffreyii* (Jeffrey pine)
Pila: *Pinus lambertiana* (sugar pine)

Keywords

Disturbance, fire ecology, fire exclusion, mechanical thinning, plant diversity, prescribed fire, shrub cover, restoration

Acknowledgments

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Abstract

Fire suppression in the western United States has significantly altered forest composition and structure, resulting in higher risk of high-severity fire and large-scale drought and bark beetle events. Mechanical thinning and prescribed fire are common treatments designed to reduce high-severity fire risk, but few studies have tracked long-term understory plant community response with repeated fire application that emulates historic fire regimes. We evaluate changes in understory plant diversity and composition and environmental characteristics over two decades following a factorial field experiment crossing thinning and two applications of prescribed fire at the Teakettle Experimental Forest (TEF) in the southern Sierra Nevada. We compare experimental fuels treatments against nearby old-growth, mixed-conifer forests with restored low-severity fire regimes in Yosemite and Kings Canyon National Parks. Although local understory plant richness initially increased most following thinning combined with prescribed fire, this treatment did not generate understory communities similar to those in nearby reference forests. Intense shrub growth resulted in low understory evenness and beta diversity over time, which a secondary burn treatment did not alter. Burning without thinning retained a more heterogeneous understory over time and, at least in the two years following the second burn treatment, with high understory richness and evenness similar to reference forest understories. Our results suggest management treatments may need to focus on creating heterogeneity in burn effects to foster diverse forest understories and limit post-treatment shrub cover.

Objectives

In this study, we evaluate changes in understory plant diversity and composition over two decades following two fuels reduction treatments at TEF in 2000-2001 and in 2017. We compare understory communities in experimental treatments against those in nearby mixed-conifer forests with active fire regimes in Yosemite and Kings Canyon National Parks (hereafter reference forests). We hypothesized that local understory plant richness, evenness, and diversity would be higher following multiple burn events relative to one or zero burn events at TEF, that multiple fires after initial thinning would best replicate understory plant community conditions at reference forests, and that the second burn would reduce heavy shrub cover established after initial thinning and burning. We further hypothesized that the observed increase in shrub cover following initial treatments may be due to expanded shrub presence in patches that were previously dominated by tree cover. Understanding the effects of introducing repeated fire into fire-suppressed forest understory communities can help researchers and forest managers improve fuel treatment practices to reduce wildfire severity while retaining rich plant diversity.

Background

Fire suppression in the western United States has significantly altered forest composition and structure, greatly increasing tree density–especially of small trees–and homogenizing stand structure and wildlife habitat (North et al., 2009; Safford and Stevens, 2017). The resulting dense, fuel-loaded forests experience higher risk of stand-replacing fire than forests with heterogeneous stand structure (Koontz et al., 2020) and are less resilient to large-scale drought and bark beetle events (Fettig et al., 2019). Both fire-suppressed and post-high severity fire conditions have resulted in homogenized forest understory microclimates in the Sierra Nevada (Ma et al., 2010; Stevens et al., 2019), where over half of California's vascular plant species are found (Potter, 1998). Fire suppression can result in an understory community dominated by species that tolerate shade and high surface fuel loads (North et al., 2005b), while high-severity fires can produce understories dominated by heavy shrub cover entrenching high-severity effects when they reburn (Coppoletta et al., 2016). Common fuels reductions treatments such as mechanical thinning and prescribed fire can not only reduce wildfire severity under moderate weather conditions (Safford et al., 2012; Stephens et al., 2009), but can also increase structural heterogeneity and understory plant diversity, at least in the short term (Abella and Springer, 2015). Initial results from long-term experimental treatments in an old-growth, mixed-conifer forest in the Sierra Nevada indicate that thinning followed by prescribed fire showed the greatest gains in understory plant richness and herbaceous cover (Wayman and North, 2007). However, these combined treatments at Teakettle Experimental Forest (TEF) became heavily shrub dominated after 11 – 15 years (Goodwin et al., 2018) similar to understory conditions following high-severity wildfire (Figure 1).

Figure 1: Heavy shrub cover that has developed in one of Teakettle's plots that was thinned and burned, 15 years after treatments. Although these treatments initially had the highest plant diversity, they now have only sparse herbaceous species. (photo credit: Malcolm North)

In contrast, a study of stands with various burn histories–but no thinning–over a 20-year period in Sequoia and Kings Canyon National Parks found that repeated use of prescribed fire restored a highly diverse understory plant community without elevated shrub cover (Webster and Halpern, 2010). Understory plant diversity is likely increased due to greater fine-scale environmental heterogeneity in these repeatedly burned forests (Halpern and Spies, 1995; McIver et al., 2013). Outside the National Parks, however, prescribed fire is often applied cautiously, resulting in low-intensity combustion. In these managed forests, thinning is often used prior to burning to provide better control of the prescribed fire's intensity and facilitate more complete, and often more uniform, burn spread (Ryan et al., 2013). It's unclear whether this pre-burn thinning facilitates the longer-term heavy shrub cover response found at TEF, and whether additional burning would restore a more diverse understory. While several experiments have examined the short-term effects of thinning and prescribed fire on understory plant diversity in mixed-conifer forests (Abella and Springer, 2015), few studies to date have assessed these changes for the same plots over multiple decades, or with repeated fire application to emulate the historic fire regime. Identifying the effects of these prescribed burns may require tracking changes at monumented sample points that experienced different intensities and number of burns.

Material and Methods

The Teakettle Experimental Forest (TEF) is an old-growth, mixed-conifer forest in the southern Sierra Nevada, located in the High Sierra Ranger District of Sierra National Forest (36°58'N, 119°2'W) (Figure 2). The study area (1,880 - 2,485 m elevation) is dominated by white fir (*Abies concolor*), red fir (*A. magnifica*), incense-cedar (*Calocedrus decurrens*), Jeffrey pine (*Pinus jeffreyi*), and sugar pine (*Pinus lambertiana*) in the overstory (North et al., 2002). Soils are predominantly poorly developed and granite-based Inceptisols and Entisols with coarse, sandy-loam texture and very low clay content. The climate is typical of the southern Sierra Nevada with hot, dry summers (17.1°C mean temperature) and cool, moist winters (1.2°C mean temperature, 1,250 mm mean annual precipitation). Fires historically occurred every 17 years on average until 1865, after which no fires larger than 3 ha occurred in TEF (Fiegener, 2002; North et al., 2005a) There is no history of significant logging prior to experimental thinning treatments, except for limited hazard tree and sugar pine removal during early white pine blister rust control efforts (North et al., 2002; Smith et al., 2005).

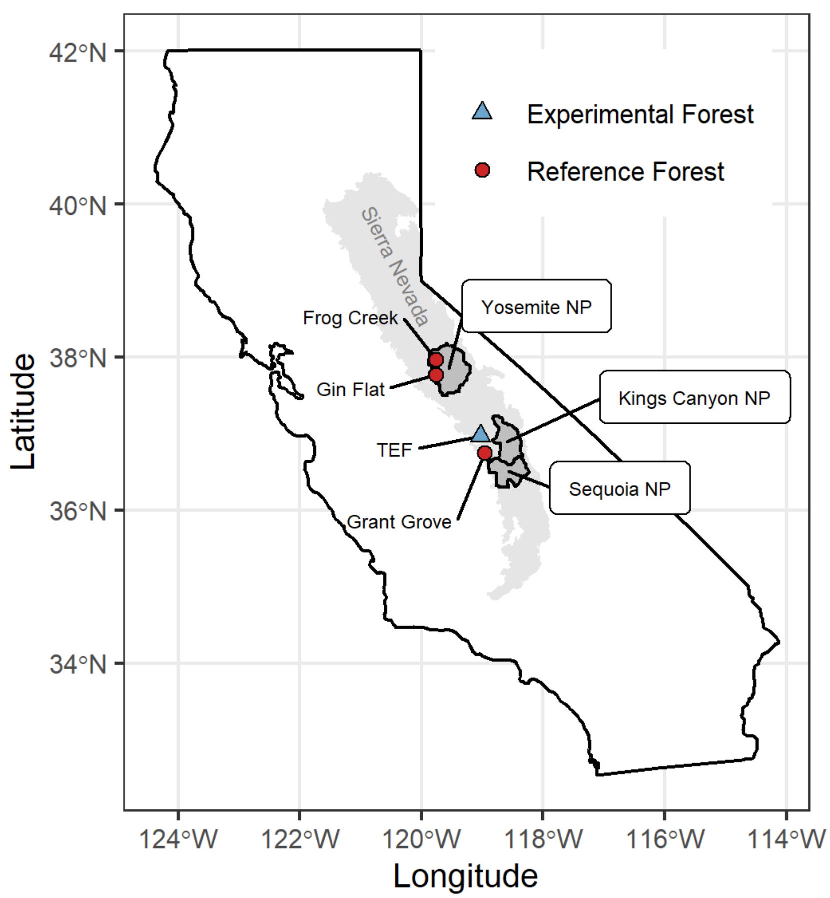

Figure 2: Map of the Teakettle Experimental Forest (TEF) and old-growth mixed-conifer reference forests with active fire regimes.

A long-term field experiment testing the effects of different combinations of burning and thinning treatments was established at TEF in 1998. Thinning treatments were: no thin, thinning all trees between 25 and 75 cm diameter at breast height as described by Verner et al. 1992 (hereafter understory thin), and a heavier thinning treatment cutting all trees >25 cm DBH but leaving 20 large (>75 cm) evenly spaced trees per hectare (hereafter overstory thin). Thinning treatments were crossed with prescribed burning and no prescribed burning for a full factorial design with 6 treatments. Each treatment was replicated in three 200 m x 200 m plots. Burn treatments were thinned in 2000 and burned in 2001, and unburned treatments were thinned in 2001. Full initial treatment details can be found in North et al. (North et al., 2002). Burn plots were re-burned in fall 2017, emulating the historic fire return interval of the site.

We identified old-growth mixed-conifer forest sites with frequent, low-severity fire regimes (hereafter reference forests) in the central and southern Sierra Nevada with similar forest type and topographic conditions to TEF. We located these sites using ArcGIS 10.6 by overlapping the mixed-conifer forest type in the CalVeg database, with a 1830 - 2290 m elevation range in the USGS National Elevation Dataset and an active fire regime consisting of at least three fires between 1960 and 2018 including at least one fire since 1990. We overlapped fire events from the CAL FIRE Fire and Resource Assessment Program's Fire Perimeter database to create polygons with unique fire histories and identify areas of low to moderate severity fire effects similar to historic fire regime conditions. We selected reference forest plots based on similar slope and aspect to TEF plots, no history of logging, geographic proximity to TEF, and multiple unique fire histories geographically close to each other. We then visited plots to confirm mixed-conifer forest overstory species composition similar to TEF.

We selected three locations based on the above criteria: Gin Flat (37°46' N, 119°46' W) and Frog Creek (37°58' N, 119°46' W) in Yosemite National Park, and Grant Grove (36°45' N, 118°58' W) in Kings Canyon National Park. See Appendix B for a full comparison of physical variables, tree species composition and understory plant composition between reference forest sites and TEF. We sampled three plots representing unique combinations of fires at each location in 2018 and 2019, as described below.

Data were collected in a nested structure within plots. Within each plot at TEF, permanent sample gridpoints were mapped in a grid using a surveyor's total station and monumented for resampling. Two replicates per treatment had nine gridpoints spaced 50 m apart and one replicate per treatment was intensively sampled at 49 gridpoints spaced 25 m apart, for a total of 402 gridpoints.

For reference forest sites, we sampled 15 gridpoints in each of the 3 plots in each location for a total of 135 gridpoints. The 15 gridpoints were arranged on a grid to fit within irregularly shaped, overlapped footprints of past fires, with 25 m (4 plots) or 50 m (5 plots) spacing between gridpoints. All gridpoint centers were marked to ensure repeated measures in the same locations. We sampled vegetation, ground cover, and environmental data within gridpoints using identical methods in TEF and reference forests, as described below.

We recorded ocular percent cover estimates for each plant species within a 10 m^2 circular area centered on the gridpoint in mid-June through early July, coincident with peak blooming period for the region. We collected unknown taxa outside of the plot and identified them using the Jepson Manual first edition (Hickman, 1993) in 1999 – 2012 and the Jepson Manual second edition (Baldwin et al., 2012) in 2013 – 2019. Taxa that could not be identified to species were identified to genus, and we identified plants within the order Poales to family. We also recorded ocular percent cover estimates for bare ground, rock, litter (<1 cm diameter), sticks (1 – 5 cm diameter), and coarse woody debris (>5cm diameter). We averaged litter depth at 3 random locations in each gridpoint. We estimated coarse woody debris cover in two categories: decay classes 1-3 and decay classes 4-5 (Maser et al., 1988). In years following burn treatments, we recorded ocular percent cover estimates for ash and char material to indicate fire extent and severity at each gridpoint. We collected vegetation and ground cover data in 1999, 2002 - 2004, 2006, 2011 - 2013, and 2016 – 2019 in TEF, and in 2018 – 2019 in reference forests.

Previous TEK studies had found three patch conditions influential on understory ecosystem processes and edaphic conditions before and after treatments (Erickson et al. 2005, Chen and North 2005, Ryu et al. 2009). We identified gridpoints that were clearly representative of these three distinct pre-treatment conditions: open (canopy closure <45%, total shrub cover <10% , n = 64), shrub dominated (canopy closure <45%, total shrub cover >30%, n = 50), and tree dominated (canopy closure > 65%, total shrub cover <10%, n = 64). We compared trends in shrub cover over time for each of these patch communities following initial treatment.

We recorded latitude, longitude, slope, and aspect at each gridpoint. Aspect was transformed to reflect difference from southwest as a relative measure of heat load using the equation $(1-\cos[\Theta-45])/2$ where Θ is the azimuth measured from true north (Beers et al., 1966).

From 1998-2017, we sampled soil volumetric water content using a Time Domain Reflectometer (TDR) with permanent installed rods at a single location in each gridpoint assessing 0-15 cm and 15-40 cm of the same soil profile(Zald et al., 2008). In 2018 -2019 we used a Fieldscout TDR 100 probe to average volumetric water content in the top 12 cm of soil in five locations for each gridpoint (at gridpoint center and 1 m in each cardinal direction) to better account for fine-scale variation in soil water content. TDR sampling locations were flagged in 2018 to ensure repeated sampling of the same soil columns.

We estimated soil depth in 2003 by pounding a rod into the soil in five randomly selected locations within 2 m of the gridpoint and taking the mean of the three greatest depths. We collected soil samples from nine gridpoints in each plot in 2003 and 2019 for nutrient and soil texture analysis. Three soil cores were taken to a depth of 30 cm with a 2 cm wide soil probe at approximately 75 cm from the gridpoint center at 0, 120, and 240-degree azimuths. When cores were not able to be taken to the full 30 cm depth, additional cores were collected from the plot until sufficient soil was collected to complete all analyses, and core depths recorded. Cores were combined in waterproof bags and kept on ice for up to 8 days. They were then air dried and analyzed by the UC Davis Analytical Laboratory for total carbon and nitrogen (Horwitz, 2010), Bray phosphorus (the recommended method for low pH soils: (Olsen and Sommers, 1982)), and particle size (2019 only, (Sheldrick and Wang, 1993)).

We assessed light availability at each gridpoint with hemispherical canopy photographs taken with a Sigma 4.5mm F2.8 EX DC HSM Circular Fisheye lens. All photographs were taken from the center of the gridpoint at breast height using a leveled tripod at dawn or dusk, with the top of the picture oriented to true north. Photographs were taken at the 402 gridpoints in TEF in 1999, 2002, and 2019, and at all 135 gridpoints in the reference forest plots in 2019. Photographs were corrected for exposure and analyzed for percent canopy cover and direct, diffuse, and total photosynthetically active photon flux density (PPFD) ($\mu mol\ s^{-1}\ m^{-2}$) using the Hemiphot.R package in R (ter Steege, 2018). For a given gridpoint, PPFD is calculated from the latitude, elevation, and the tracking angle of the sun over the course of a year. We used PPFD values as an approximation of the relative difference in understory light conditions between gridpoints. All data analysis was performed in R version 3.6.3 (R Development Core Team, 2011), unless otherwise noted.

Plant diversity metrics were calculated using the vegan package in R (Oksanen et al., 2019). Gridpoint-scale richness, diversity [antilog Shannon-Wiener diversity index (Jost, 2006)], and evenness (diversity / richness), were calculated at each gridpoint in each year. We calculated average beta diversity—the difference in species composition between locations—within each plot in each year. We chose the Raup-Crick dissimilarity index for beta diversity because it helps to differentiate variation in community dissimilarity from variation in local richness by comparing pair-wise differences in species composition to a null model (Chase et al., 2011; Raup and Crick, 1979).

We compared understory plant diversity, richness, evenness, beta diversity, and shrub cover as a function of treatment type and time period (pre- and post-initial treatment and pre- and post- second entry fire). Due to the non-normal distribution of plant diversity, cover, and environmental data, we used the non-parametric Friedman's Test with Bonferroni corrected post-hoc Wilcoxon's tests to compare repeated measures of our response variables over time within treatments, with gridpoint as the grouping variable for repeated measures.

We compare treatment outcomes with reference forest conditions by comparing gridpoint-scale diversity, richness, evenness, and shrub cover in all TEF treatments and reference forests with recent fires (3-7 years old), and reference forests with older fires (13 - 20 year old fires). We use Kruskal-Wallis tests with Bonferroni corrected Dunn's post-hoc tests to identify differences in conditions between treatments and reference forests two years after second-entry burn treatments at TEF.

Gridpoints were classified as either locally burned (at least 1% ground cover as ash or char) or unburned (less than 1% ground cover as ash or char) following initial treatments and second-entry burns. Mean and standard deviation for shrub cover, and average litter depth were calculated for burned and unburned gridpoints in each thinning treatment before and after initial treatments and second-entry burns.

We fit multi-level Bayesian linear regression models using the brms package (Bürkner, 2017) to compare effects of burn and thin treatment combinations on changes from pre-treatment values in local richness, evenness, and diversity following initial treatments in 2000 and 2001 and second burn treatments in 2017. In each model, we include random effects for plot and year, with fixed effects for thin treatments, number of burn events, and their interactions as predictor variables. To assess differing treatment effects over time, we compare models without time, and with linear and polynomial terms for time since disturbance using leave-one-out cross validation (Vehtari et al., 2017). Burn and thin treatment effects on response variables were compared using pairwise contrasts of posterior samples of estimated marginal means with the emmeans package in R (Lenth, 2020).

We use weakly-informative, regularizing priors in all models to aid in model convergence and avoid biasing our posterior distribution towards extreme parameter values. Joint posterior distributions were sampled using MCMC sampling with 3 chains of 2000 iterations, and 1000 warm-up samples. We diagnosed model convergence using trace plots and Gelman-Rubin diagnostic values < 1.01 for all model parameters.

Results and Discussion

Thinning and burning effects on understory plant diversity over time differed by both treatment type and diversity metric (Figure 3). After the initial (2000-2001) treatments, thin-burn treatments increased local richness the most (adding a median 2-3 species per gridpoint), and the burn-only and overstory thin treatments displayed smaller, but still significant increases

(Wilcoxon's post hoc of the Friedman test, adjusted $p < 0.05$). Evenness, however, decreased significantly in the overstory thin treatment following initial treatments (Wilcoxon's post hoc of the Friedman test, adjusted $p < 0.05$). For gridpoint-scale diversity ($e^{H'}$) (combining richness and evenness), the largest increases occurred in the thin-burn treatments following initial treatment, with smaller, but significant increases in other treatments (Wilcoxon's post hoc of the Friedman test, adjusted $p < 0.05$).

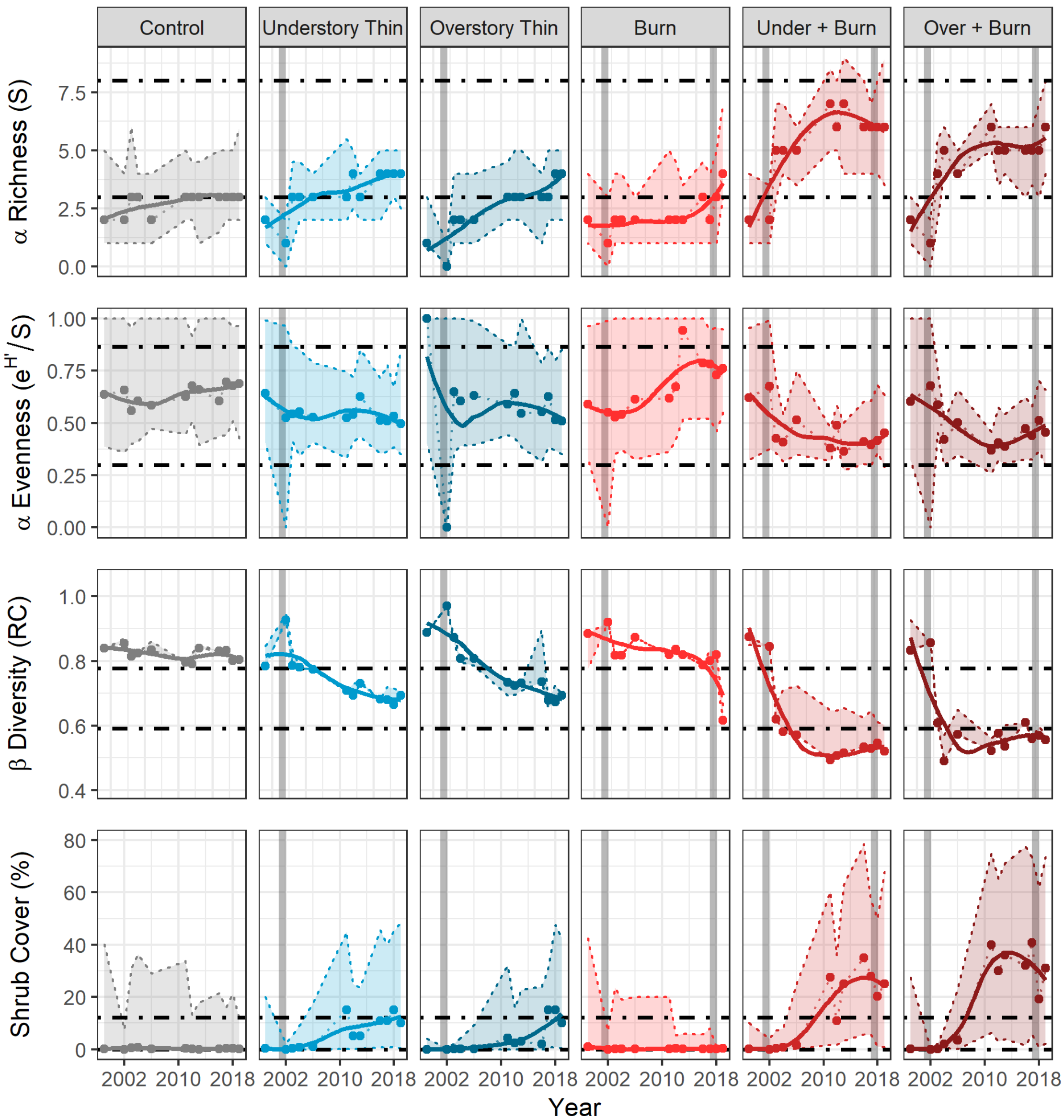

Figure 3: (Top to bottom) local richness, local evenness, beta diversity, and shrub cover over time for experimental treatments in Teakettle Experimental Forest. Horizontal black dashed lines represent the middle 50% of values in reference forests with active fire regimes for comparison to TEF treatments. Vertical gray lines represent timing of initial treatments in 2000-2001 and second-entry prescribed fire in 2017. Points represent median values in each year, bold lines represent a smoothed trend in median over time (Loess smoothing function, median ~ year), and colored areas represent the middle 50% of values for each year.

In contrast, the second-entry burn (2017) significantly increased gridpoint-scale richness in the burn-only and overstory thin-burn treatments (Wilcoxon's post hoc of the Friedman test, adjusted $p < 0.05$), but there was no significant increase in the understory thin-burn treatment. Gridpoint-scale evenness ($e^{H'}/S$) did not change significantly for any treatment following second-entry fire, with the burn-only treatment retaining significantly higher evenness than all thinned treatments (Dunn's post hoc of the Kruskal-Wallis test, adjusted $p < 0.05$). Following the second burn, gridpoint-scale diversity ($e^{H'}$) increased most in the burn-only treatment (+1.2 effective species on average) due to increased richness and high evenness, with smaller but still significant increases in the overstory thin-burn treatment (Wilcoxon's post hoc of the Friedman test, adjusted $p < 0.05$).

Initially (2002-2006) thin-burn treatments did approximate gridpoint-scale richness in reference forests following treatment, but with reduced evenness and beta diversity (Figure 3). Thin-only and burn-only treatments did not reach richness levels typical of reference forests at any point in the 16 years following initial treatment. However, the burn-only treatment did roughly match the local diversity (both richness and evenness), and beta diversity of reference forests in the years following a second burn event.

Reference forests with more recent fires (3-7 years old) showed higher local richness and diversity, but somewhat lower evenness, beta diversity, and shrub cover than sites with older fires (13-20 years old). This is in contrast to our thin-burn treatments, which show declining evenness and beta diversity over time. Shrub cover in thin-burn treatments roughly approximated recently burned reference forests for a few years, but rapidly increased to levels much higher than reference forests after 10 years post-treatment.

In 2019, following the second-entry burn treatments, the overstory thin and burn treatment had significantly higher canopy openness, direct light, and diffuse light than reference forests, and understory thin and burn treatments were significantly higher in all three light characteristics than reference forests with recent fires (Table 1). Following initial treatments, the burn-only treatments and control had significantly lower canopy openness, direct light, and diffuse light than reference forests, and the overstory thin and burn treatment was significantly higher in all light conditions than reference forests with recent fires. No other thin treatments differed significantly from reference forest light conditions.

		TEF Treatment						Reference Forest		Kruskal-Wallis Test	
Environmental Variable	Year	Control	Understory Thin	Overstory Thin	Burn	Under + Burn	Over + Burn	Old Fire	Recent Fire	sig	P Value
Direct Light (PPFD) (µmol s-1 m-2)	2003	14.2 a (5.99)	16.4 ab (5.31)	19.0 b (6.41)	14.4 a (5.73)	17.5 ab (5.11)	22.3 c (4.02)			*	2.4E-17
	2019	14.8 e (6.69)	16.3 ce (5.90)	19.9 bd (6.73)	17.3 cde (6.00)	22.4 ab (5.57)	24.4 a (4.50)	19.4 bcd (5.42)	17.8 cde (4.77)	*	4.31E-24
Diffuse Light (PPFD) (µmol s^-1 m^-2)	2003	0.98 b (0.33)	1.21 a (0.26)	1.38 a (0.32)	0.93 b (0.30)	1.30 a (0.27)	1.60 c (0.24)			*	5.82E-32
	2019	1.05 c (0.36)	1.18 cd (0.30)	1.39 b (0.36)	1.19 bcd (0.36)	1.64 a (0.33)	1.76 a (0.28)	1.4 b (0.36)	1.32 bd (0.27)	*	7.93E-36
Soil Moisture (% VWC)	2003	8.33 ac (7.85)	9.23 b (4.01)	11.8 bc (10.3)	7.25 a (5.80)	9.51 abc (5.38)	7.42 abc (3.21)			*	1.29E-6
	2019	6.10 c (8.17)	4.70 bc (6.46)	4.84 abc (7.28)	4.29 abd (8.40)	4.72 abc (6.88)	1.89 d (1.67)	2.7 ad (3.61)	2.87 ad (4.18)	*	7.44E-10
Litter Depth (cm)	2003	3.21 bd (3.16)	2.89 abd (2.81)	3.61 d (3.18)	1.66 a (1.80)	1.77 ab (1.66)	0.71 c (1.14)			*	1.69E-14
	2019	4.88 d (3.15)	5.44 d (3.27)	4.37 bd (3.18)	1.55 c (1.62)	3.12 ab (2.26)	2.49 ac (1.96)	2.66 abc (2.05)	2.43 ac (1.88)	*	3.33E-21

Table 1. Mean values for environmental variables following initial treatments (2003) and second-entry burn treatments (2019) across all treatment types at Teakettle Experimental Forest.

Standard deviations are shown in parentheses. Asterisks indicate unequal mean rank values for an environmental variable across treatments in a given year (Kruskal-Wallis test, $p < 0.05$). Different letters following mean values indicate significant pair-wise differences between treatments (Bonferroni corrected Dunn's post-hoc analysis, $p < 0.05$).

Following the second application of prescribed fire in burn treatments at TEF, litter depth in burned gridpoints did not significantly differ from reference forests, regardless of initial thinning treatment while Teakettle control gridpoints had significantly higher litter depth than burned plots at Teakettle and in reference forests. Burn-only gridpoints had significantly lower total soil C than reference forests, and significantly lower total soil N than reference forests with older fires. No treatments had significantly different soil P than reference forests.

		Initial Treatment			Second-Entry Fire		
Variable	Thin Treatment	# Gridpoints	Before	After	# Gridpoints	Before	After
Shrub Cover (%)	No Thin	Burned (17)	22.82 (33.75)	6.84 (16.97)	Burned (23)	13.27 (21.03)	7.10 (17.22)
		Unburned (50)	23.47 (32.64)	14.15 (24.51)	Unburned (44)	5.92 (14.26)	2.50 (6.47)
	Understory Thin	Burned (48)	23.18 (42.65)	6.47 (17.67)	Burned (15)	31.15 (31.36)	10.43 (18.94)
		Unburned (19)	9.13 (33.00)	6.17 (13.26)	Unburned (52)	37.06 (33.09)	38.94 (32.69)
	Overstory Thin	Burned (51)	16.95 (29.42)	2.52 (7.74)	Burned (15)	36.39 (35.08)	16.58 (24.97)
		Unburned (16)	17.95 (29.86)	4.28 (9.20)	Unburned (52)	44.21 (36.01)	39.03 (35.62)
Litter Depth (cm)	No Thin	Burned (17)	6.47 (4.49)	1.76 (1.76)	Burned (23)	3.77 (2.75)	0.87 (0.80)
		Unburned (50)	3.53 (3.54)	2.07 (2.13)	Unburned (44)	3.21 (2.13)	1.31 (1.69)
	Understory Thin	Burned (48)	5.55 (5.34)	1.62 (1.55)	Burned (15)	3.22 (1.87)	1.59 (1.67)
		Unburned (19)	2.64 (2.75)	1.81 (1.85)	Unburned (52)	3.03 (3.17)	2.63 (2.14)
	Overstory Thin	Burned (51)	5.69 (5.78)	0.74 (1.12)	Burned (15)	1.85 (1.29)	1.10 (1.19)
		Unburned (16)	2.60 (1.93)	0.72 (1.01)	Unburned (52)	2.51 (1.90)	2.29 (1.96)

Table 2. Summary of fire effects for plots targeted for burning in initial experimental treatments and second-entry fire treatments, by initial thinning treatment. Effects are displayed separately for burned and unburned 10 m2 gridpoints. Mean values are displayed with standard deviations in parentheses.

Second-entry prescribed burning produced small changes in understory diversity and did not significantly reduce shrub cover (Figure 3). To better understand these results, we examined fire behavior in both the first and second applications. Fire did not uniformly impact plots within the burn treatments, and the two burn events showed different patterns of fire across treatments. The understory thin-burn treatment experienced noticeable fire (≥ 1% ground cover of ash and char) at 72% of gridpoints in 2001, and only 19% of gridpoints in 2017 (Table 2). Similarly, the overstory thin-burn treatment experienced noticeable fire at 76% of gridpoints in 2001, and only 24% of gridpoints in 2017. The burn-only treatment experienced noticeable fire at only 25% of gridpoints in 2001 and 36% in 2017. The initial burn treatment in 2001 burned extensively in the thinned plots, with less effect on the un-thinned plots, while the opposite pattern is true in the second prescribed burn event in 2017.

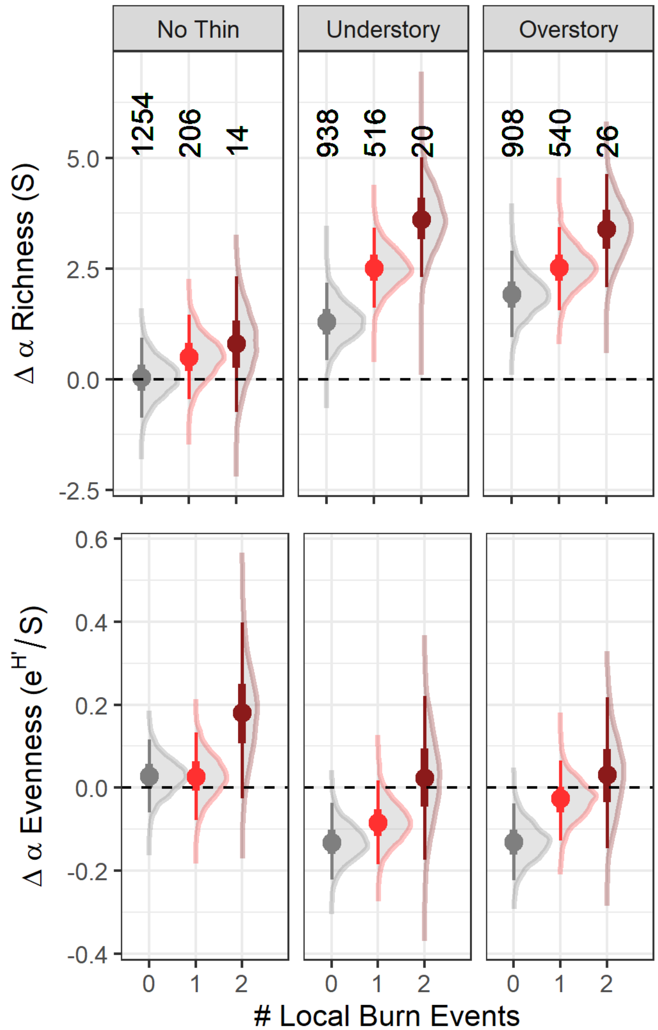

Figure 4: Posterior draws of estimated marginal means from Bayesian hierarchical models of change in local ($10m^2$ gridpoint-scale) understory plant richness (S) and evenness ($e^{H'}/S$) as a function of thinning treatment and number of local burn events (inferred from presence/absence of burned ground cover following each burn), with random effects for plot and year. Points and intervals indicate median and 50% and 95% credible intervals for model fits for each treatment. Shaded areas indicate distributions of posterior linear predictions for each. Number of data points in each group is indicated in black.

Given the small number of gridpoints that burned in each plot during the second fire event, we group gridpoints based on presence/absence of burned groundcover following each fire event to model effects of repeated fire on plant diversity at the local, 10 m^2 gridpoint scale. Draws from the joint posterior distribution of our hierarchical Bayesian models indicate that richness and evenness responded differently to thinning and burning (Figure 4). Contrasts of estimated marginal means of linear predictions for the effect of burn number and thinning treatment on richness, and evenness in the 2 – 18 year period following initial treatment indicate that experiencing one fire is much more likely to result in a greater increase in local richness than no fire, especially in thinned treatments ($p = 0.0077$ for no thin, $p < 0.0001$ for understory thin, and

$p = 0.001$ for overstory thin). The small number of gridpoints that experienced two fire events in understory thin treatments were much more likely to experience greater increases in richness than their unburned ($p < 0.0001$) and once-burned counterparts ($p = 0.0193$). Gridpoints that experienced two fires in overstory thin treatments were also more likely to result in greater increases in richness than no fire ($p < 0.0001$), and somewhat more likely than those with one fire event ($p = 0.0373$). This evidence supports our hypothesis that repeated fires increase understory plant richness at the local scale.

Gridpoints with one or more burn events were only more likely to experience more positive changes in evenness than unburned gridpoints in the overstory thin treatment ($p < 0.0027$ for one burn event and $p = 0.0297$ for two burn events). In contrast, both thin treatments resulted in a more negative change in evenness ($p = .0073$ for understory thin and $p = .013$ for overstory thin), but one or two burn events reduce this effect and there was little difference between understory and overstory thinning treatments. Both thinning treatments with and without fire had a significant non-linear effect on richness over time, peaking ~12 years after disturbance.

Due to large observed difference between shrub cover in thin-burn treatments at TEF and reference forests, we investigated possible associations between initial conditions and shrub growth at TEF. We classified sample gridpoints into three patch conditions which initial research at Teakettle found were associated with different functional and compositional responses (North et al., 2002)—open (canopy closure <45%, total shrub cover <10% , n = 64), shrub dominated (canopy closure <45%, total shrub cover >30%, n = 50), and tree dominated (canopy closure > 65%, total shrub cover <10%, n = 64) patches—and tracked shrub cover over time in individual gridpoints following each level of prescribed thinning with and without fire.

We found little change or slight increases in shrub cover in the open gridpoints regardless of thin or burn treatment, and a gradual return to near original shrub cover in shrub dominated gridpoints that were thinned, regardless of burn treatment. (Figure 5). Although very few un-thinned gridpoints actually burned in the initial prescribed fire (n = 17), all but one of these burned gridpoints maintained or decreased their shrub cover. The largest increases in shrub cover were observed in previously tree-dominated gridpoints after thinning, and those which also burned showed earlier and larger increases in shrub cover. Teakettle's significant increase in shrub cover appears to be most associated with a vigorous shrub response when thinning reduces cover in tree-dominated patches.

This study points to key differences in how treatments affect plant understory diversity. Although local understory plant richness initially increased most following thinning combined with prescribed fire, this fuels reduction treatment did not generate understory communities most similar to those in reference old-growth, mixed-conifer forests with frequent, low-severity fire regimes. Intense shrub growth after thinning, and especially thinning followed by fire (Goodwin et al., 2018), resulted in low understory evenness and beta diversity over time, which a secondary burn treatment emulating the historic fire return interval did not alter. High shrub response may be driven by fire's stimulation of seed germination and resprouting, and augmented by thinning's reduction in live tree basal area which reduced competition for light, belowground water, and nutrients (Goodwin et al., 2018; Halpern, 1989). In contrast, multiple burns without thinning retained a more heterogeneous understory more similar to reference forest understories, with high local richness, local evenness, and beta diversity, at least in the two years following the second burn treatment. In the burn only treatment, low levels of shrub cover created by dispersed, discrete patches actually increased understory evenness and created more variable fire effects. Our results suggest management treatments may need to focus on creating heterogeneity in burn effects to foster diverse forest understories and limit shrub cover.

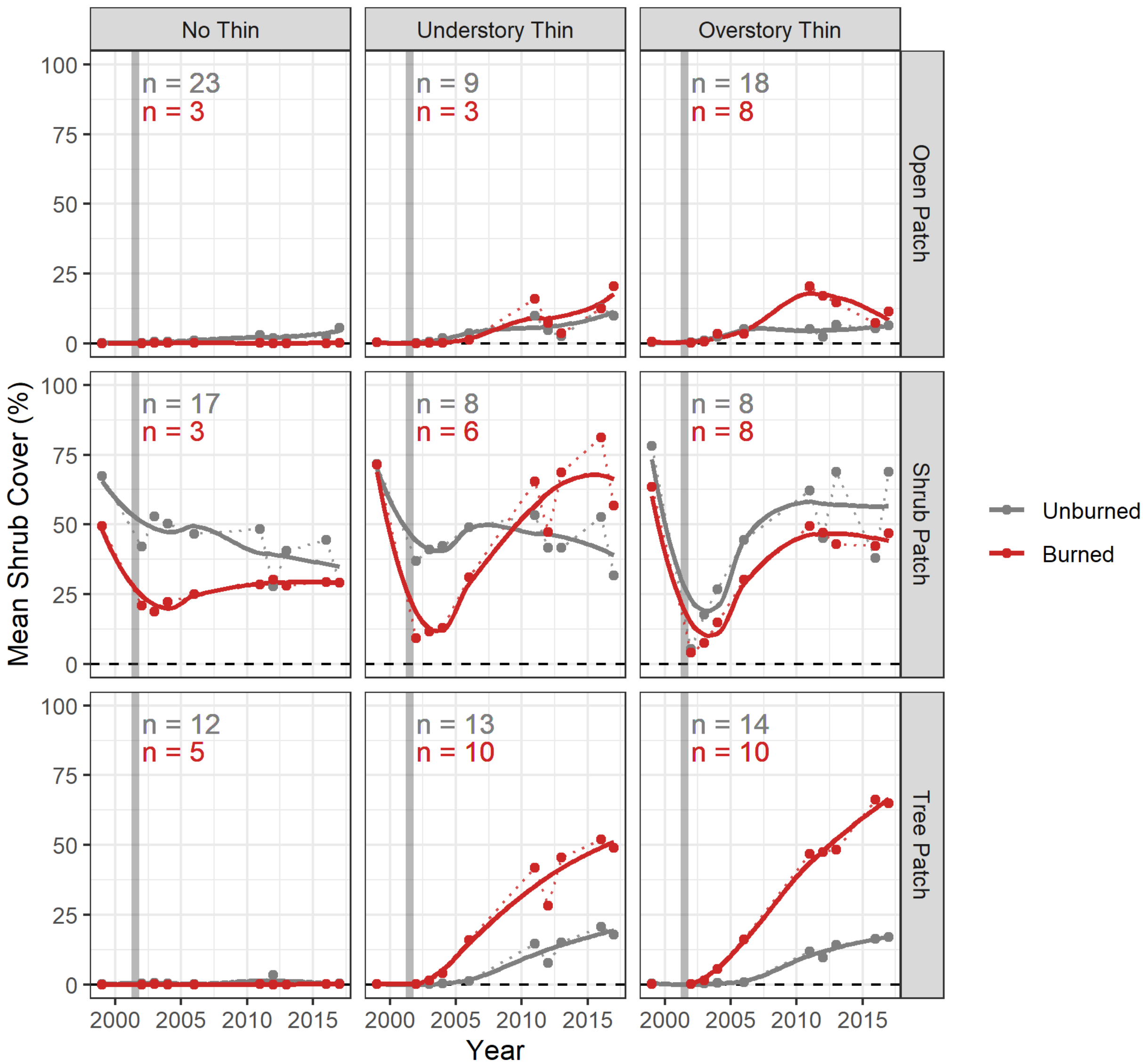

Figure 5: Mean shrub cover over time in gridpoints that were originally open patches (canopy closure <45%, total shrub cover <10% %, n = 64), shrub dominated patches (canopy closure <45%, total shrub cover >30%, n = 50), and tree dominated patches (canopy closure > 65%, total shrub cover <10%, n = 64) prior to treatment. Gridpoints are further separated by thinning treatment and whether they burned in the initial burn treatment. Thin dashed lines and points represent median shrub cover values for each year and solid lines represent the Loess-smoothed median shrub cover over time. Vertical gray lines represent initial thinning and/or burning treatments in 2000 – 2001. The number of gridpoints for each combination of thin treatment and original patch type is shown for unburned gridpoints (gray) and burned gridpoints (red) in the upper left corner of each panel.

This study has several limitations to consider. First, replication is limited in this type of large-scale field experiment, resulting in low statistical power for comparing plot-level metrics. We try to address this limitation by using hierarchical models that take advantage of the nested structure of our study design. Second, reference sites for mixed-conifer forests with intact or restored fire regimes are rare (Lydersen and North, 2012) and pose challenges for relevant understory comparisons because individual species may or may not be shared in species pools across locations. We attempted to address this limitation by selecting reference sites as similar as possible to TEF conditions (elevation, slope, aspect, overstory composition, dominant shrub species). We also limit our use of reference site comparisons to define a range of variation for mid-elevation mixed-conifer forest stands with what is often considered target conditions for forest restoration treatments. Third, we have limited data following the second burn, and we saw from the initial treatments that there is a strong temporal component to understory response. We can only compare the initial effects of the second burn, and we expect that the effects will continue to change over time.

Understory community response varied greatly between the first and second burn events, likely due to different fire behavior in 2001 and 2017. The second burn only had a major response in the un-thinned treatment, and very little effect in the two thinned treatments. We suspect that this may be due to cool, high humidity conditions during the burn and high moisture in shrubs dampening combustion. Local richness and local evenness showed conflicting trends in our study, indicating that many of the sites that gained species locally following thinning and prescribed fire also became more dominated by a small subset of similar species across sites. Other studies have also suggested different metrics of diversity frequently show divergent responses to disturbance, even when presenting the results from the same experiment (Li et al., 2004; Svensson et al., 2012).

We found some support for our hypotheses that multiple burn events would increase local understory plant richness and evenness relative to one or zero burn events at TEF. Gridpoints that did experience more fire did show increased local richness, but more fire only increased evenness in the most heavily thinned treatments (Figure 4). We may only see treatment-level increases in the burn-only treatment because so few of the gridpoints in the thin-burn treatments actually burned in the second fire. This difference in burn behavior often occurs between repeated prescribed fire applications (Waring et al., 2016) and highlights how variable second-entry fire can be due to fuel loading and shrub response following the first burn. Compounding these effects, fuels were elevated in the burn-only plots because mortality from California's 2012-2016 drought was higher in these stands due to their higher density (Steel et al., n.d.). Our results suggest that for managed forests where prescribed burning is often cautiously applied, understory restoration may require more time and repeated burning.

Our comparison of understory plant communities at TEF and Reference forests did not support our hypothesis that multiple fires after initial thinning would best replicate understory plant community conditions at reference forests. Although thin-burn treatments increased local richness and diversity the most following initial treatment, they only briefly approximated recently burned reference forests and quickly diverged (Figure 4). Their lower evenness and beta diversity, as well as their considerably higher shrub cover do not closely match conditions in reference forests with older fires, where near-zero median shrub cover indicates that shrubs remain concentrated in discrete patches rather than widespread.

The observed trends in understory community diversity after initial treatment in this study are correlated with the growth of shrubs as an understory dominant and a shift toward open shrub-dominated community types over ~10 – 12 years following thinning and burning. Contrary to our hypothesis, the second burn treatment did not substantially reduce shrub cover in any of our treatments.

Other studies of understory communities and shrub cover have found shrubs to be a major driver of understory plant richness and diversity after wildfires over multiple decades (Bohlman et al., 2016; Webster and Halpern, 2010) This large increase in shrub cover in our thin-burn treatments may be analogous to conditions following wildfires in similar mixed-conifer forests, where high severity fire and shrub cover can create a positive feedback loop that induces type conversion from conifer forest to an alternate stable state of montane chaparral (Coppoletta et al., 2016). Results from TEF's thin-burn treatments agree with a recent analysis of understory diversity in Sierra Nevada yellow pine and mixed-conifer forests following different fire severities, in which moderate - high severity patches (>50-75% basal area mortality) had the highest richness and diversity, but evenness and beta diversity declined with greater fire severity, with fire-stimulated *Ceonothus cordulatus* as an indicator species for moderate-high severity fire (Richter et al., 2019). Despite relatively low levels of crown scorch in initial burn treatments compared to a high severity wildfire (Innes et al., 2006), thin-burn treatments may emulate high-severity burn conditions by releasing shrubs from competition with trees while stimulating their abundant soil-banked seed and sprouting from fire (Halpern, 1989; Huffman and Moore, 2004).

Conclusions and Management/Policy Implications

Patchiness within prescribed fire treatments may be beneficial to maintaining diverse understories across larger spatial scales. Congruent with other studies of understory plant community response to fire in mixed-conifer forests, more intensive patches of fire maximize benefits to local richness in areas with reduction in litter and increases in light availability, while temporarily reducing shrub cover. While these treatments became more homogeneous at the 4 ha plot scale over time, spatial and temporal variability in fire behavior may maintain beta diversity in the landscape by retaining closed, mesic understory communities. Such heterogeneity in fire history could support greater phylogenetic plant diversity by increasing the abundance and richness of plants from the southern-xeric biogeographic affinity in local patches while providing habitat refugia for plants from north-temperate biogeographic affinity (Stevens et al., 2015). This also fits with the recently proposed framework that increased pyrodiversity, or diversity of fire histories, at the landscape scale supports increased biodiversity (He et al., 2019).

Conversion from mixed-conifer forest to shrub-field communities is an undesirable outcome of high severity wildfire for many forest managers in the Sierra Nevada, and would be an unintended outcome for forest restoration and fuels reduction treatments designed to reduce the risk of high-severity fire in these forests. A previous understory analysis in the TEF found shrub cover positively correlated with reduction in live tree basal area associated with thinning and subsequent mortality in the 2012 - 2016 drought (Goodwin et al., 2018).

In fire-suppressed forests, significant shrub cover increases following mechanical thinning and burning treatments are a management concern because of their reduction in understory diversity and potential to increase subsequent fire intensity if burned when shrubs are dry. While the sample sizes in our preliminary analysis of shrub response in open, shrub and tree dominated gridpoints are small (Figure 5), results suggest a possible explanation for the conversion of thinned and burned plots at TEF to heavy shrub cover. Fire may have stimulated the seed bank of dominant shrubs *Ceanothus cordulatus* and *Actostaphylos patula*, after decades of seed accumulation due to fire suppression. meanwhile, both fire and mechanical thinning may facilitate new shrub growth in sites previously occupied by trees whose shade precluded shrubs. Previous research at TEF has shown that trees often occupy the best growing condition microsites, particularly those with deeper soils that contain higher soil moisture (Meyer et al., 2007) in contrast to open areas with high surface temperatures and scant soil moisture. More research is needed to investigate this pattern but our results do suggest caution for managers using mechanical thinning. Removal of small trees that have infilled sites in fire-suppressed forests may not trigger an aggressive shrub cover response, but removal of large trees, which often indicate wet, productive sites (Fricker et al., 2019), could facilitate rapid shrub expansion into microsites where low-light conditions from tree cover previously precluded shrub expansion.

Restoring understory conditions may not happen after a single prescribed burn, regardless of initial thinning. Our results agree with long-term monitoring of understory response to multiple fires in mixed-conifer forests in Sequoia and Kings Canyon National Parks, where understory plant diversity responses often needed long time periods (10 – 20 years) after fire or even multiple fire events to become fully apparent (Webster and Halpern, 2010). Restoring the understory conditions and plant communities in fire-suppressed mixed-conifer forests may take multiple treatments over many years.

Future Research

The Teakettle Experiment was set up to follow long-term ecological responses to common fuel reduction treatments. All the gridpoints are permanently monumented facilitating repeat measurements. We will continue to follow the understory plant community response to treatments to assess longer term responses and we will re-apply prescribed burns on a schedule commensurate with the historical fire regime (17-year fire return interval). Lacking future funding, we will opportunistically use summer field crews from other ongoing research at Teakettle to conduct the annual sampling every five years and following particularly dry and wet climatic years. We will continue to publish these results and expect to have future manager field trips to see how the treatments continue to respond over time.

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Appendix A: Contact Information for Key Project Personnel

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Appendix B: List of Completed Publications, Thesis and Conference Presentations

Articles in peer-reviewed journals

Odland, M.C., J.J. Goodwin, B.V. Smithers, M.D. Hurteau, and M.P. North. 2021. Plant community response to thinning and repeated fire in Sierra Nevada mixed-conifer forest understories. Forest Ecology and Management 495: 119361.

Graduate Thesis

Odland, M.C. 2021. Plant community response to thinning and repeated fire in Sierra Nevada mixed-conifer forest understories. Graduate Group in Ecology, Department of Plant Sciences, University of California, Davis.

Conference Presentations

Odland, M. 2020. Understory plant communities after thinning and prescribed fire in a Sierra Nevada mixed-conifer forest. University of California, Davis, Ecology Graduate Student Symposium.

Odland, M. 2019. Understory plant communities after thinning and prescribed fire in a Sierra Nevada mixed-conifer forest. *Ecological Society of America annual meeting. August 15 2019, Louisville*, KY USA

Appendix C: Metadata

Metadata for the understory sampling of the Teakettle gridpoints and the reference forest plots has been provided to J.F.S.P via uploading.